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Effect of spatial differences in growth on distribution of seasonally co-occurring herring *Clupea harengus* stocks

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RUNNING HEADLINE

GROWTH AND DISTRIBUTION OF HERRING

ABSTRACT

The mechanisms most likely to determine the distribution of the two major herring *Clupea harengus* stocks in their common early summer feeding ground in the Eastern North Sea, Skagerrak and Kattegat were investigated through analysis of acoustic survey data from six consecutive years. No change was detected in biomass of North Sea Autumn Spawning *C. harengus* (NSAS) over time whereas the biomass of Western Baltic Spring Spawning *C. harengus* (WBSS) severely declined. Analyses of centre of gravity by stock showed no change in NSAS distribution, whereas the WBSS changed to a more western distribution over time. Contrary to previous perception of the juvenile migration, NSAS were found to leave the study area already at the age between 1 and 2 and WBSS 1 year olds were encountered in the Skagerrak. The estimated parameters of von Bertalanffy growth equations showed marked differences between areas with fish in the eastern part of the area having the lowest size at age at all ages. Further, their growth conditions appeared to deteriorate progressively over the period studied. Both NSAS and WBSS showed the highest condition in the North Sea and Skagerrak while condition was substantially lower in Kattegat. The westward movement of spring spawners over time suggests that growth rate and possibly density of conspecifics influences the migration pattern and distribution of *C. harengus* in the area. In contrast, there was no evidence to suggest that distribution was constant over time within stocks or that distribution reflected size dependent limitations on migration distance.

KEY WORDS: Acoustic surveys, Skagerrak, condition, migration, stock identity

INTRODUCTION

Atlantic herring *Clupea harengus* (L.) exhibit marked diversity over their distribution range, often showing complex population structures with both genotypic and phenotypic variation (Bekkevold *et al*., 2005; Ruzzante *et al*., 2006) and a wide variety of migration patterns and growth forms (Secor *et al*., 2009; Brunel & Dickey-Collas, 2010). Often two or more *C. harengus* stocks are targeted by a single fishery exploiting shoals of mixed population origin (Rosenberg & Palmén, 1982; Clausen *et al*., 2007a; Payne *et al*., 2009) and population-specific exploitation rates may vary strongly both within and between years in response to combined effects of the spatial distribution of the fishery, spatio-temporal variation in the degree of population mixing and the relative biomass of the individual populations (Bekkevold *et al*., 2011). The degree of mixing between stocks is often variable and unpredictable which challenges successful spatio-temporal fishery management, particularly when populations are asynchronous in population dynamics (Payne *et al*., 2009). In these cases, it may be necessary to restrict fishing on one stock while the other stock can potentially sustain a larger fishing pressure. Managing fisheries of distinct *C. harengus* stocks is essential for several reasons: to maintain yields in the area, and to avoid stock depletion of the weaker component; and also to ensure the unique ecosystem function of *C. harengus* remains intact. One possibility is to use spatial management measures (Kell *et al*., 2009), but in order for this to be successful, knowledge of what determines the migratory behaviour and also the degree of mixing in different areas is essential.

C. harengus in the Skagerrak, the Kattegat and the Western Baltic (Figure 1) consist of a mixture of migrating populations with different life history characteristics. Of these, the populations within the North Sea Autumn Spawner stock (NSAS) and Western Baltic Spring Spawner stock (WBSS) are dominating summer foraging aggregations (Bekkevold *et al*., 2011). The two *C. harengus* stocks are

52 targeted by a fishery in the Skagerrak and the Kattegat as well as the eastern parts of the North Sea
53 exploiting shoals of mixed population origin (Rosenberg & Palmén, 1982; Payne *et al*., 2009; Clausen
54 *et al*., 2007b). The two populations follow specific migration patterns. Spawning of the WBSS occurs
55 in February-May with the most important spawning ground at the Greifswalder Bodden off the island
56 of Rügen (Biester 1979) where hydrographical retention keep larvae near local nursery areas in the
57 Western Baltic sea (Polte *et al.,* 2013). The majority of the 2+ winter ring (wr) WBSS *C. harengus* are
58 assumed to migrate out of the subdivision 24 for the summer feeding grounds in Division IIIa and the
59 eastern North Sea (Payne *et al.,* 2009). During autumn, the WBSS return to the southern part of the
60 Kattegat with the majority of the stock overwintering in the Sound (ICES subdivision 23) (Biester,
61 1979; Otterlind, 1987; Nielsen *et al*., 2001). NSAS *C. harengus* larvae, hatched in autumn along the
62 UK east coast and in winter in the English Channel, drift from the spawning areas to subsequently
63 metamorphose in spring near the nursery area ranging from the eastern North Sea into to the Skagerrak
64 and the Kattegat (Burd, 1978; Heath *et al*., 1997). NSAS are assumed to remain in this area until 2 wr
65 when they start to mature and join the adult population feeding aggregation in the central and northern
66 North Sea (Corten, 1986).

67 Atlantic *C. harengus* populations are often highly migratory with migration distance varying from a
68 few 100 km to more than 1000 km (Slotte, 1999; Alerstam *et al*., 2003). These migrations are assumed
69 to be adaptations to the local environmental conditions for increased success in spawning, growth or
70 survival of offspring and/or maturing individuals. Migration take advantage of spatial and temporal
71 differences in the distribution of resources (being food, spawning habitat availability, shelter for
72 predators, etc.), and thus increase the fitness of the migrants (Harden Jones 1968; Chapman *et al*.,
73 2012). For such behaviour to evolve, the benefits of using two or more different areas during a defined

74 time-cycle must outweigh the costs of the migration. *C. harengus* may use predictive (genetic factors or
75 learning) and reactive (response to near field or state-space comparisons) orientation mechanisms
76 during migration (Harden Jones 1968, Fernö *et al*., 1998). A combination of reactive and predictive
77 orientation mechanisms may provide *C. harengus* with a flexible migration strategy, adapted to both
78 predictable and unpredictable conditions (Fernö *et al*., 1998). The underlying behavioural mechanism
79 could be influenced by ‘‘enviroregulation’’, as suggested for *scombrids* (Reid *et al*., 1997), where the
80 fish select their immediate environments by swimming towards ‘preferred’ environmental conditions.
81 For *C.harengus* it has been shown that the intra-annual as well as inter-annual spatio-temporal pattern
82 of migrations may vary due to e.g. changes in environmental conditions (Fréon and Misund, 1999;
83 Dingle & Drake, 2007), abundance (Fernö *et al*., 1998), fish age (Harden Jones, 1968; Fréon &
84 Misund, 1999), condition (Slotte, 1999) or geographic variation in food availability (Kvamme *et al*.,
85 2003).

86 The WBSS migration has been characterised as a summer feeding migration from spawning areas
87 distributed in fjords, sils and lagoons to the open waters of Kattegat and in particular the Skagerrak and
88 Eastern parts of the North Sea (Figure 1), followed by a return to wintering areas (Nielsen *et al*., 2001;
89 Payne *et al*., 2009). An age-related migration distance gradient has been reported for WBSS (Payne *et*
90 *al*., 2009) with the older individuals migrating furthest into the outermost area of the Skagerrak and
91 into the North Sea where the feeding conditions are supposed to be optimal (Maar *et al*., 2013).
92 However, given the several factors that have been shown to impact migration of *C.harengus*, the
93 variability in migration distance (from the main spawning ground in the Western Baltic to the optimal
94 feeding grounds in the outer Skagerrak, Figure 1) between years for WBSS could depend on other
95 factors than age. They e.g. may migrate further to get to the optimal feeding grounds when they are in

96 better than average condition. Alternatively, migration distance may be determined by local carrying
97 capacity, in which case the proportion migrating towards attractive areas is higher when abundance is
98 low. It has been shown for NSAS that the preferred spawning more Southern spawning grounds are
99 used independent of the stock size, while the less preferred more Northern grounds are used when the
100 stock size is increasing (Corten 2001). Thus abundance related habitat selection may be occurring in
101 *C.harengus* as it has been shown for other species (e.g. *Gadus morhua* in the North Sea (Blanchard *et*
102 *al*., 2005).

103 The present study examines the observed distribution, growth and condition of *C. harengus*
104 encountered in the mixed feeding aggregations in the Eastern North Sea, the Skagerrak and the
105 Kattegat during summer. From the distribution of NSAS and WBSS during six consecutive years of
106 acoustic surveys, the migration mechanisms most likely to determine the early summer distribution of
107 the age classes of the two major stocks were investigated. The analysis tested four hypotheses to
108 understand mechanisms and implications of stock mixture in the summer feeding area:

109 H1: Migration is predetermined by predictive orientation mechanism (genetic factors or imprinting)
110 towards predefined areas typically characterised by bottom topography and persistent hydrographical
111 features acting as an attractor. Thus the distribution of a population will appear constant, albeit with
112 random variation.

113 H2: Migration is directed towards the area showing optimal growth conditions.

114 H3: Migration is size dependent with larger fish migrating further than small. Thus the proportion of
115 individuals of WBSS in the North Sea will have a larger body size on average than the individuals
116 encountered in the Kattegat, closer to the main spawning site.

H4: Migration is a result of local carrying capacities. In this case, the abundance of NSAS and WBSS in the preferred area will seem constant independent of total *C.harengus* abundance while vary in other areas.

METHODS

SURVEY DATA

Hydro acoustic survey data on distribution, size and weight at age for *C. harengus* in the Kattegat and the Skagerrak was available for the years 2006 to 2011. The acoustic survey is part of the ICES Coordinated Acoustic Survey in the Skagerrak and Kattegat, the North Sea, West of Scotland and the Malin Shelf area (ICES, 2012).

Acoustic data were collected using a 38 kHz echosounder with the transducer mounted in a towed body towed at a target depth of 4-5 m depth. The raw acoustic data were pre-integrated into 1 m depth samples for each ping and combined into 1 nautical mile datasets. The acoustic data were scrutinized in depth layers for each nautical mile using special judging software which allows ignoring data from layers and/or intervals with noise. In areas with acoustic input from plankton and jellyfish, manually adjustable thresholds were applied to eliminate echoes from these objects. Final integration was conducted from 3 m below the transducer to 1 m above the bottom or to a maximum depth of 150 m. The area with depth above 150 m contributes to 31 % of the entire survey area. The integration yielded the total backscattering cross section, s_A, of fish per square nautical mile for each nautical mile along the survey track.

For each ICES statistical rectangle, a mean areal back scattering, s_A-value, was calculated based on the s_A-values for all sampled nautical mile inside the area. This value is assumed to represent the whole ICES statistical rectangle and is multiplied with its total area to obtain the total backscattering cross section of fish in the ICES statistical rectangle. Based on allocated trawl hauls in each ICES statistical rectangle or, if necessary, hauls from nearby ICES statistical rectangle, the species and length composition of fish were identified. The mean back scattering cross section, TS, for fish in the subarea was estimated based on the relative composition of fish in the mean catch and the length dependent TS-relationships of *C. harengus, S.spratus, Gadoid sp* and *S. scombrus* (ICES, 2012). The total number of fish in the subarea is then the total backscattering cross section of fish divided by the mean scattering cross section of fish. The number of fish per species is assumed to be proportional to the contribution of the given species in trawl hauls.

For each haul used for identification of species and length composition, the total catch was weighed, sorted into species and total weight and length distribution per species was recorded. Clupeids were measured to the nearest 0.5 cm total length below, and weighed to the nearest 0.1 g wet weight. In each trawl haul 10 (if available) *C. harengus* per 0.5 cm length class were sampled and frozen for individual laboratory determination of length, weight, age, and spawning type (NSAS or WBSS).

BIOLOGICAL PARAMETERS

In the laboratory, the length stratified subsamples of *C. harengus* were thawed and total length (nearest mm) and wet weight (0.01 gram) was recorded for each fish. The number of otolith winter rings (WR) was determined using the procedure described in ICES (2003) and entered as a proxy for age. The reason for using winter rings and not age in years is that the *C. harengus* are spawned either in autumn (NSAS) or spring (WBSS) and given that the NSAS only have approximately 3 months to live before

158 they experience their first winter, their first winter ring is not recordable and their first visible winter
159 ring is actually their second experienced winter (where they thus are 1.5 years old). The WBSS on the
160 other hand are less than 1 year old, when they lay down their first recordable winter ring. Otolith
161 microstructure (OM) was used to separate *C. harengus* stocks according to their different hatching time
162 using visual inspection of season-specific daily increment pattern in the larval otolith (Mosegaard &
163 Madsen 1996; Clausen *et al*., 2007b). The method discriminates between sympatric *C. harengus* with
164 different spawning times (Brophy & Danilowicz, 2002, 2003; Clausen *et al*., 2007b). Separation of
165 North Sea *C. harengus* from Western Baltic *C. harengus* in the Kattegat, the Skagerrak and the eastern
166 North Sea follows the assumption that all North Sea *C. harengus* are autumn/winter spawners and all
167 Western Baltic *C. harengus* are spring spawners as multiple populations with similar spawning time
168 cannot be distinguished with this analysis alone (Clausen *et al*., 2007). From 2010 onwards, harmonic
169 coefficients from Elliptic Fourier Analysis (EFA) of silhouette otolith images and non-parametric
170 nearest neighbour Discriminant Analysis (DA) were used together with OM to classify production
171 samples after calibration with an OM determined known-stock base-line (Burke *et al*., 2008). The OM
172 analysis is assumed to have less than 5% misclassification error of the base-line (Clausen *et al*., 2007b)
173 and cross-validated self-assignment shows about 10% misclassification of the EFA based DA of the
174 production samples (ICES, 2013a).

175 DISTRIBUTION

176 Changes in distribution over time were evaluated using two different methods. Firstly, the yearly
177 biomass across winter ring groups by ICES statistical rectangle for each area and spawner type was
178 investigated to determine whether a trend over time could be detected. Secondly two indicators of
179 distribution were estimated; the centre of gravity of location by stock and age and changes in the area

180 covered were investigated by estimating the average squared distance. The former indicator reflects
181 whether the distributional area has changed geographical location whereas the latter indicator reflects
182 changes in the area covered by the stock. Centre of gravity was calculated by the mid-point latitude and
183 longitude in each ICES statistical rectangle weighted by the biomass of age categories in each ICES
184 statistical rectangle:

185 $$\left(C_{lon,s,y,t}, C_{lat,s,y,t}\right) = \left(\left(\sum_{i=0}^{N} B_{s,y,t,i} lon_i\right)\left(\sum_{i=0}^{N} B_{s,y,t,i}\right)^{-1}, \left(\sum_{i=0}^{N} B_{s,y,t,i} lat_i\right)\left(\sum_{i=0}^{N} B_{s,y,t,i}\right)^{-1}\right)$$

186 Where $C_{lat,s,y,t}$ and $C_{lon,s,y,t}$ is the latitude and longitude of the center of gravity of spawner type *s* with *t*
187 winter rings in year *y*, $B_{s,y,t,i}$ is the biomass of spawner type *s* with *t* winter rings in year *y* in the *i*th
188 rectangle and lat_i and lon_i is the mid latitude and longitude of ICES rectangle *i*, respectively.

189 Changes in the area covered were investigated by estimating the average squared distance, *D*, of a
190 biomass unit to the centre of gravity:

191 $$D_{s,y,t} = \left(\sum_{i=0}^{N} B_{s,y,t,i}\left(\left(lat_i - C_{lat,s,y,t}\right)^2 + \left(lon_i - C_{lon,s,y,t}\right)^2\right)\right)\left(\sum_{i=0}^{N} B_{s,y,t,i}\right)^{-1}$$

192 This index is proportional to the area covered by 95% of the biomass if the distribution is a two-
193 dimensional normal distribution in space and even when the distribution is skewed or in other ways
194 deviate from normality, this indicator still reflects concentration of the stock (Rindorf & Lewy, 2012).
195 The indicator is not responsive when the distribution is bimodal, but judging from the distribution, this
196 was not a problem in our analyses.

Age related changes in the combined effects of mortality and migration were investigated by general linear models of log(numbers) at age by area and type to compare slopes of the observed decline in numbers with expected total mortality to infer immigration and emigration patterns among areas (F-test, assuming normal distributed observations, McCullaugh & Nelder 1989).. The difference in slope between cohorts, years and areas were also investigated to determine whether different cohorts experienced differences in mortality. Further, the presence of higher declines for older ages, corresponding to higher mortality or emigration, was tested by estimating a second degree polynomial relationship between age and log(numbers at age).

GROWTH BY AREA

The difference in length at age between area and spawner type was investigated to determine which of the areas could be considered most favourable for growth or alternatively attract a specific growth type. This was done through comparing length at age in a specific area with length at other ages and estimating a von Bertalanffy growth equation across all years. This method will provide a combined estimate of the effect of growth, size selective mortality and size specific net migration in an area. The analysis is referred to here as an analysis of growth, which pertains to the assumption that size specific net migration are of minor importance in comparison to growth in our results. This assumption is discussed when interpreting the relationship between apparent growth and changes in distribution.

The relationship between area and spawner type and length at age was estimated through analyses of the parameters of the von Bertalanffy growth equation using data from all years ignoring any cohort or year effects. Von Bertalanffy growth equation for all areas and types was estimated as follows:

$$L_{a,s,t,i} = L_{\infty,a,s}\left(1-\exp\left(-K_{a,s}(t-t_{0,a,s})\right)\right)+\varepsilon_i$$

218 Where *t* denotes number of winter rings, $L_{a,s,t,i}$ is the average total length in the *i*th observation (ICES
219 rectangle) at *t* winter rings in area *a* and spawner type *s*, $L_{\infty,a,s}$ is the average length of very old *C.*
220 *harengus* in area *a* and spawner type *s*, $K_{a,s}$ is the growth rate in area *a* and spawner type *s*, $t_{0,a,s}$ is the
221 theoretical age at which length is zero in area *a* and spawner type *s* and ε_i is an error term,
222 $\varepsilon_i \in N(0,\sigma_\varepsilon)$. Parameters were estimated by least squares and recorded lengths at age 0 wr were
223 excluded from analyses. The effect of the factors area *a* and spawner type *s* on the parameters was
224 evaluated using an F-test and a significance level of 0.01. This lower significance level was chosen to
225 accommodate the fact that the observations were not strictly independent (within-year correlation, see
226 results) and to avoid including factors which, though significant, explain a very low amount of the
227 variation. The length anomaly of the individual observation was defined as the residual length from the
228 estimated von Bertalanffy relationship and was calculated and used for further analyses of yearly
229 differences. Length-anomalies were investigated for trends by estimating the parameters in a
230 generalized linear model, investigating the effects of type and year for each area separately assuming a
231 normal distribution of anomalies.

232 CONDITION

233 An average condition index was calculated for each type, year, statistical rectangle and age by first
234 estimating the common weight-length relationship

$$W = aL^b$$

for all observations using a generalized linear model with gamma distributed error in mean weight to estimate b. The average condition, C_i of a given combination of type, year, statistical rectangle and age (observation i) was then estimated as

$$C_i = W_i L_i^{-b}$$

The difference in condition between spawner types, years and areas was investigated using ANOVA whilst the trend over time in a generalized linear model with year as a linear variable, and the effect of length on condition by area was tested between immature and mature *C. harengus* of both spawner types using the same method.

RESULTS

DISTRIBUTION

C. harengus distribution at different scales was variable among years (Figure 2) as was the annual proportion of spawner types by square. Analysis of distribution by year shows that the total distribution and relative abundance shifts between years based on data collected during the summer acoustic cruise (Figure 2), thus *C.harengus* do not necessarily congregate in the same area each summer. Total biomass of spring spawners has been decreasing over the period in Kattegat (correlation between year and biomass per rectangle=-0.58, $P<0.0001$) and Skagerrak (correlation between year and biomass per rectangle=-0.30, $P<0.01$) (Figure 3). In contrast, there was no significant trend in the biomass of spring spawners in the North Sea or in biomass of autumn spawners in any area ($P>0.20$ in all cases, Figure 3). The decline in total biomass of spring spawners over the time period was 81.4% in Skagerrak and

95.9% in Kattegat. As the biomass declined over time, the proportion of the total biomass for the area which constituted spring spawners decreased accordingly. This decrease was significant in both the North Sea ($P<0.05$) and Kattegat ($P<0.01$), but was below the significance level in Skagerrak ($P>0.05$).

The shift in distribution is also seen when examining the centre of gravity of the two spawner types (Figure 4); there is no change in either latitude or longitude of the centre of gravity of autumn spawners ($P>0.50$ in both cases). On the other hand, the longitude of the centre of gravity decreased significantly for the spring spawners in the period corresponding to a westward shift in distribution (correlation=-0.40, $P<0.05$) whereas there was no significant change in latitude of center of gravity ($P>0.23$). The centres of gravity by age class were significantly positively correlated along the latitudinal component ($r=0.61$, $P<0.001$), primarily driven by an age class related tendency of old *C. harengus* to be located in more Northern (deeper waters) in Skagerrak and the North Sea (Figure 4). No such correlation existed along the longitudinal dimension, but spring spawners had a significantly more easterly distribution than autumn spawners for all ages ($P<0.0001$). The distribution coverage (*D*) of the two stocks showed year effects but no trend and coverage was not significantly correlated to biomass ($P>0.16$ in all cases).

Abundances expressed as log transformed numbers declined linearly with increasing age (Figure 5). Slopes for autumn spawners exhibited no area effects ($P>0.1$), corresponding to a similar combined effect of mortality and migration in all areas, whereas a significant area effect on slopes for spring spawners was found ($P<0.0001$). Slopes were significantly non-linear for autumn spawners ($P<0.0001$), whereas no significant non-linearity was found for spring spawners ($P>0.1$) that this pattern is also found in the North Sea indicate that migration to all feeding areas generally takes place in all age

groups including 1 wr. Slopes for autumn spawners were overall steeper (slope=-1.37 (se=0.09)) than for spring spawners and substantially higher than the estimated F (fishing mortality) + M (natural mortality) (0.66) in stock assessment would suggest (ICES, 2013b) indicating either a higher mortality or an emigration of autumn spawners. All slopes were highly significant (P<0.01). Spring spawners in the Skagerrak and the North Sea exhibited declines which were lower than those expected from stock assessment estimates of total mortality (0.39 (se=0.11) and 0.58 (se=0.07), in the North Sea and Skagerrak, respectively), whereas spring spawners in the Kattegat had a significantly higher negative slope (1.14 (se=0.09)) indicating either emigration from Kattegat to Skagerrak of the North Sea or substantial differences in mortality between areas.

COMPARISON OF DISTRIBUTION, GROWTH AND SIZE AT AGE

Von Bertalanffy K and t_0 did not differ significantly between spawner types or between areas (P>0.01 in all cases), whereas L_∞ differed both between spawner types and areas (P<0.0001 in both cases). This indicates that length at age is similar for the youngest ages but becomes increasingly different between types and areas with age (Figure 6). The variation in L_∞ between areas explained 49% of the residual variation in mean length around a common von Bertalanffy relationship, and variation in L_∞ between spawner types another 11%, leading to a total of 60% of the residual variation explained by the final model. The estimated L_∞ in the North Sea did not differ significantly from that in the Skagerrak (P>0.1). However, to avoid introducing a growth period related bias in the subsequent analyses (see methods), separate estimates were derived from the two areas. The resulting parameter estimates can be seen in Table 1. The variables L_∞, K and t_0 were highly correlated (all correlations>0.75) as is generally the case when estimating von Bertalanffy parameters.

296 The growth anomalies (the residuals from the reduced von Bertalanffy model) did not differ
297 significantly between spawner types in any of the areas (P>0.09 in all areas, Figure 7) and there was no
298 significant differences between years in the North Sea (P>0.1). However, the residuals varied
299 significantly between years in the Skagerrak and Kattegat (P>0.005 and P<0.0005, respectively). The
300 year effect in residuals violates the assumption of independent residuals and hence the degrees of
301 freedom used when reducing the von Bertalanffy model are likely to be overestimated and parameter
302 error estimates are likely to be minimum estimates. In the Skagerrak, the differences did not result in a
303 trend over time (P>0.20), whereas the difference between years in Kattegat introduced a significant
304 negative trend in residuals (P<0.0001) with the average residual decreasing by 0.38 cm per year.
305 Hence, the Kattegat fish not only had the lowest L_∞ and hence the lowest size at age at all ages, this
306 measure also declined progressively over the time period.

307 CONDITION

308 Condition differed significantly between spawner types (P<0.0001) with condition being $0.12*10^{-3}$
309 $g*cm^{-3.26}$ (std=$0.02*10^{-3}$ $g*cm^{-3.26}$) higher in autumn spawners than spring spawners. The difference
310 between areas was also highly significant (P<0.0001), with both types showing the highest condition in
311 the North Sea and the Skagerrak while condition was substantially lower in the Kattegat (Table 2). A
312 significant correlation was found between condition of the two spawner types by ICES rectangle year
313 and age within all age groups with 1 wr having the highest correlation r=0.81 p<0.0001, and in all cases
314 r>0.4, P<0.05 (Figure 8).

315 Condition decreased significantly with age ($-0.070*10^{-3}$ $g*cm^{-3.26}$ per year, standard error=$0.007*10^{-3}$
316 $g*cm^{-3.26}$) with no significant difference in the decrease between areas (P>0.1) or spawner types

317 (P>0.5). No significant correlation between condition by age class and biomass per ICES rectangle was
318 found for any of the two spawner types, indicating local density independence of condition.

319 For both spring and autumn spawners condition decreased significantly with age. In addition to a
320 significant area effect (P<0.0001), spring spawners exhibited a significantly different relationship with
321 residual length for juvenile and adult spring spawners over all areas, showing a non-significant
322 negative slope for 1-2 wr and a significant positive slope for 3-5 wr (slopes -0.06, R^2=0.06 and 0.21,
323 R^2=0.33 respectively, P<0.005 for slopes being equal). No trends in condition with growth rate and no
324 significant differences between juveniles and adults were found in autumn spawners (P>0.1).

325 ## DISCUSSION

326 This study showed significant variation in the distribution of western Baltic spring spawners and North
327 Sea autumn spawners in their summer feeding area, rejecting the hypothesis that the summer feeding
328 migration of these two stocks in the study area is predetermined by predictive orientation mechanism
329 (H1). *C. harengus* in the Skagerrak and the Eastern North Sea were in general significantly larger than
330 in the Kattegat and the former areas exhibited consistently higher abundance than Kattegat. Spring
331 spawners migrated to the Skagerrak and the North Sea from 1wr whereas autumn spawners appeared in
332 all three areas from the earliest age but started to leave all areas at least between 1 and 2 wr. Size at
333 age did not differ between areas at 0 wr, but differences emerged with increasing age, supporting the
334 conclusion of differences in growth rate while indicating that migration was at least not initially size
335 dependent. Thus the migration appeared to be size dependent directed towards the area showing
336 optimal growth conditions, confirming hypotheses H2 and H3 of this study. Density in the low growth
337 area Kattegat decreased substantially faster than could be explained by the expected mortality levels,

corresponding with a density dependent migration towards areas where growth rate appears to occur at a faster rate or an increased emigration as growth conditions deteriorated. This indicates that the summer feeding migration is a result of local carrying capacities given that the abundance of NSAS and WBSS in the preferred area was independent of total *C.harengus* abundance while it significantly decreased with total abundance in Kattegat; thus confirming hypothesis H4 of the study.

Estimated biomass for spring spawners declined substantially in both the Kattegat and the Skagerrak over the period, whereas no trends were found for autumn spawner biomasses in any of the three areas. The cause of the decline was likely a combination of high fishing pressure and decreasing recruitment during the first decade of the 2000s (ICES, 2013b). The spring spawners apparently kept migrating as far as the North Sea at the same time as they became fewer and smaller at age in the Kattegat, thus the remaining part of the stock seemed to prefer feeding areas further from the spawning grounds regardless of initial size**.** Areal coverage of the spring spawning stock did not co-vary with decreasing biomasses and thus did not follow the hypothesis of contracting feeding range with declining population size (Murphy, 1977).

The North Sea and Skagerrak parts of the summer-feeding area were at a constant advantage in terms of the largest size at age and the highest condition across years, independent of spawning type. The difference in L_∞ between the North Sea-Skagerrak and the Kattegat was around 3 cm for both spawning types and even in years with positive size at age anomaly in the Kattegat, they still exhibited the smallest size as the anomaly never exceeded 1 cm (Table 1, figure 7). Thus, the Eastern North Sea-Skagerrak likely provided the best growth opportunities for *C. harengus* irrespective of spawning type and year. *C. harengus* is known to be a size selective planktivore, preferring large-sized e.g. calanoid zooplankton species, as seen in the Baltic (Flinkman *et al*., 1998), the North Sea (Maravelias *et al*.,

2000; Last, 1989; Segers *et al*., 2007) the Norwegian Sea and the North Atlantic (Dalpadado *et al*., 2000; Gislason & Astthorsson, 2002) and the Gulf of St. Lawrence (Darbyson *et al*., 2003). The available literature and data on the zooplankton community in the Kattegat-Skagerrak area suggest that higher concentrations of egg producing adult stages of the *Calanus finmarchicus* (Gunnerus) follow frontal zones coupled to the Skagerrak loop of Jutland current and low saline waters entering the Skagerrak from the Kattegat (Maar *et al*., 2013). Also, the community of larger zooplankton changes in the transition zone between the Baltic and the North Sea; euphausiids increase significantly in size from Kattegat to Skagerrak (Buchholz & Boysen-Ennen, 1988). Thus supremacy in food quality and availability in the Eastern North Sea-Skagerrak may explain at least some of the difference observed here in growth pattern between areas.

C. harengus biomass dominates the pelagic fish community in the Skagerrak and surrounding areas, but *C. harengus* condition and apparent growth rate exhibited divergent co-variation with *C. harengus* abundance in the three sub-areas. There was an increase in condition in the North Sea and Skagerrak concurrent with the decrease in biomass in the Skagerrak, whereas both condition and size at age of spring spawners in Kattegat decreased over the time-period concurrently with a marked decrease in biomass. Evidence of density dependent growth has been found for several stocks e.g. Icelandic summer spawners (Oskarsson, 2008), Norwegian spring-spawners (especially for immature fish; Toresen, 1990), Georges Bank (Melvin & Stephenson, 2007), and Baltic Sea Atlantic *C. harengus* (Casini *et al*., 2006), but not for others (Gulf of Finland, and southern Gulf of St Lawrence, as reviewed in Melvin & Stephenson (2007). *C. harengus* in the Eastern North Sea and Skagerrak did not display any trend in growth rate over time. In contrast, the condition of *C. harengus* in the Kattegat was consistently poorer than that of *C. harengus* in the Skagerrak and the Eastern North Sea across years

382 and spawning type, which supports the conclusion that Kattegat is less optimal for summer growth. The
383 opposing trends in condition in Kattegat and Skagerrak concurrent with the order of magnitude
384 decrease in the Kattegat and Skagerrak biomasses also indicates that the decrease in size at age in the
385 south-eastern part of the summer distribution area is unrelated to density dependence in the two stock
386 sub units.

387 A decrease in length at age also acts to decrease biomass. However, the decrease in asymptotic length
388 in Skagerrak and Kattegat was 1.7 cm and 2.2 cm, respectively, corresponding to about 18% and 25 %
389 decrease in individual weight, which is clearly insufficient to explain the 81% and 96% decrease in
390 biomass in the Skagerrak and the Kattegat, over the entire time period. The latest stock assessment
391 estimates of the total Western Baltic Spring Spawner total biomass shows a decline of 47% from 2006
392 to 2011, whereas North Sea Autumn Spawner total biomass has increased by about 17% (ICES,
393 2013b). A marked difference in size selectivity and intensity of both fishery and natural predators in
394 Kattegat compared to Eastern North Sea and Skagerrak could also explain the change in biomass and
395 different growth rate pattern. However, since 2002, the *C. harengus* fishery in the area has been
396 concentrated in the more north-western part of Skagerrak (ICES, 2013b). Although the predation field
397 may differ between the areas, it seems unlikely that predators should be responsible for an increasing
398 outtake of larger *C. harengus* in the Kattegat only and hence be the cause of the decreasing length at
399 age.

400 A significant year effect on residual length in both the Kattegat and the Skagerrak is only matched by a
401 similar cohort effect in the Skagerrak, indicating that the stock components in the Kattegat are not
402 persistent among years and they most likely redistribute to the Skagerrak at older ages This is further
403 supported by the much steeper slope of the log transformed cohort numbers for both spawning types in

404 the Kattegat. The variation in annual center of gravity for both stocks in the area is much greater than
405 for the autumn spawners' center of gravity in the North Sea during the same period and time of the year
406 (ICES, 2013b). The lack of correlation between biomass and distributional trends in the transition area
407 indicates that the search for the best feeding opportunities shifts the population distribution annually.
408 This is overlaid by a westward migration tendency of the autumn spawners and a gradual shift towards
409 deeper waters with increasing size for both spawning types. Hence, changes in biomass levels and
410 centres of gravity as well as patterns in size at age all point to a redistribution of *C. harengus* towards
411 more north-western parts of the summer feeding area during a period when the spring spawner
412 population declined. The observed population mobility among years indicates that local changes in
413 environmental conditions may be the drivers behind the general distribution pattern.

414 Sudden density dependent changes in growth rate are not uncommon in *C. harengus* and may appear as
415 a regime shift mediated through interspecific clupeid competition as in the Baltic (Möllmann *et al*.,
416 2005) or intraspecific competition in the Gulf of Riga (Raid *et al*., 2010) where an increase in *C.*
417 *harengus* abundance in the late 1980s changed growth conditions to much smaller maximum size at
418 age. Further, a large *C. harengus* year-class may suppress the individual growth in the cohort and exist
419 as a marker for the entire life span as seen for the 1904 year-class of Norwegian spring spawners (Hjort
420 1914) and the 2000 year-class of the North Sea autumn spawners (ICES, 2013b).

421 The two *C. harengus* stocks in the area exhibit marked differences in their innate migration behaviour
422 that probably reflect stock-specific differences in spawning time and location. Autumn and winter
423 spawned *C. harengus* larvae drift during winter from the western and southern parts of the North Sea
424 towards their later nursery areas including the transition area of the eastern North Sea, the Skagerrak
425 and the Kattegat (Johannesen & Moksness 1988). Larvae from the spring spawning stock are dispersed

426 locally (Polte *et al*., 2013) and juveniles therefore actively have to migrate to the nursery grounds in the
427 transition area.

428 The proportion of spring spawners increases at 2 wr compared to 1 wr in the Eastern North Sea part of
429 the summer feeding area (ICES, 2013b), and it has therefore generally been assumed that the full
430 migration distance of the spring spawning stock is first attained at 2 wr (Payne *et al*., 2009). However,
431 our analysis of slope of log abundance at age with no significant nonlinearity in spring spawners
432 indicates that 1 wr spring spawners migrate as far towards the North Sea as their older relatives. The
433 higher slope in the corresponding analysis of autumn spawners indicate that juveniles of this stock
434 leave the nursery area in high numbers already between 1 wr and 2 wr, leading to an increase in spring
435 spawner proportion from 1 wr to 2 wr in the Eastern North Sea area.

436 During the growing season, juvenile *C. harengus* join schools of similar sized individuals (Nøttestad *et*
437 *al*., 1999). The findings here indicate that initially juveniles from both stocks form mixed schools in the
438 area and gradually relocate according to experienced growth potential. A higher occurrence of mixed
439 juvenile schools in the summer feeding area early in life when the two *C. harengus* types are of the
440 same size would explain the higher correlation in condition between spring and autumn spawners at 1
441 wr. Further the lack of positive correlation between condition and residual size in juvenile spring
442 spawners as opposed to adult spring spawners could be explained if spring spawner juveniles with the
443 highest growth potential would school with the largest and fastest swimming autumn spawner
444 juveniles.

445 The apparent advantage in terms of growth rate associated with the western parts of the summer
446 distribution area would mean that to optimize growth, individual *C. harengus* should spend the summer

447 feeding period there. As the difference in size at age in the two areas in terms of both length and
448 condition increased over time, the distribution concurrently shifted towards the high growth areas
449 (Figure 7). Given that the autumn spawners did not systematically shift distribution over time, the
450 distribution of the *C. harengus* biomass did not simply follow a given distribution of food items. Thus
451 for the spring spawners, the determining factor for the amplitude and direction of the summer feeding
452 migration is likely to differ from the determinant of the autumn spawner distribution.

453 The summer feeding migration pattern observed in the spring spawners appears to be consistent with
454 maximization of growth rate in the individual *C. harengus* where *C. harengus* with increasing age and
455 size progressively abandon the sub optimal feeding areas in the Kattegat to concentrate further to the
456 north-west. State dependent migration is a well-known behaviour in fish (Harden Jones, 1968) and for
457 *C. harengus* it has been well documented for Norwegian Spring Spawning *C. harengus* both
458 concerning spawning migration (Slotte & Fiksen, 2000) and summer feeding migrations (Kvamme *et*
459 *al*., 2003). In our study, the extent of the migration is probably defined at an early stage since the
460 differences in growth rates in the areas emerge with age (Figure 6). Thus the advantage in terms of
461 growth rate continues through life for the individuals reaching furthest in the migration. However,
462 given the westerly change in distribution over time (Figure 4) during the years where the growth
463 conditions in Kattegat continues to worsen, indicates that this pattern can change and *C. harengus* can
464 benefit from improved opportunities for growth by changing their migration pattern, just as seen in
465 Norwegian Spring Spawners (Kvamme *et al*., 2003). The observed westward changes in distribution of
466 the spring spawning *C. harengus* may be caused either by increased mortality of fish in Kattegat, by a
467 general decrease in the stock combined with an increase in the migration distance of the average fish or
468 by a combination of the two. An increase in migration could be induced by generally increased size at

age or by the diminishing density dependent competition for resources in Skagerrak/North Sea as density decreases. The former seems unlikely as length at age residuals decreased in both Skagerrak and Kattegat, indicating that the fish did not need to have a threshold condition/size to move to Skagerrak. In that case, size at age would have remained unchanged in Skagerrak. There could be indications of a threshold size to move to the North Sea as no change in residual length was seen here. If density dependent competition for resources has limited migration of smaller fish so far, this effect should diminish in Skagerrak in later years, given the reduction in biomass recorded, leaving room for more fish to move to this area. If these fish were among the larger fish in Kattegat, this movement would act to decrease length at age in both Skagerrak (now receiving smaller fish) and Kattegat (now losing larger fish). If the effect is furthermore the result of accumulating effects on length at age at different ages, this could explain why biomass in an individual year in spite of underlying density dependent effect was not significantly related to residual length. Thus, a degree of size dependence of migration distance may still exist though this does not show up in the current investigation.

The advantage in terms of growth rate in western areas and the westward displacement of the distribution of spring spawners over time suggests that both growth rate and density of conspecifics may influence the migration pattern of WBSS *C. harengus*. In a trade-off between migration expenditure and energy accumulation for growth and later reproduction local *C. harengus* with a low growth potential (expressed as a lower condition in all years) will not experience a net energy gain by increasing migration distance and moving further out than Kattegat, displaying the same differences in trade-off between migration length and spawning success as observed in migrating and non migrating *C. harengus* in a Norwegian fjord (Johannesen *et al*., 2009).

This study demonstrates a growth related migration of both spring and autumn spawners directed towards the more western parts of the summer feeding area, where the growth conditions are optimal. This is a change in the perception of the mixture of *C. harengus* during summer in the area and it will have consequences for the management of the fishery on these stocks during summer. The fishery in the area takes mixed catches of juveniles from the two stocks whereas adult *C. harengus* in the catches predominantly consist of spring spawners. The results of this study imply that catches of *C. harengus* in these areas with optimal growth conditions will consist of a faster-growing part of the stocks, which should be considered by the management of the *C. harengus* fishery. A mixed fishery targeting specific parts of a stock may lead to a reduction in the capacity of the stock to withstand climate variability and change; i.e. the resilience of the stock (Schindler et al., 2010). The distribution of the *C. harengus* in the area is thus more influenced by growth of the individual fish than the age of the fish. The change from the earlier perception of a limited 1 wr migration (see Payne *et al*., 2009) to a full dispersion of all juvenile spring spawners to the entire summer feeding area, combined with the finding of progressive juvenile autumn spawner emigration will lead to different mixing of the stocks in juvenile fishery than previously assumed. This will influence the current procedure of predicting catch options to be considered in the management of the *C. harengus* by-catch in the small meshed sprat fishery in Division IIIa (ICES 2013a) given the need for considering the varying mixture of juvenile *C. harengus*. This study, thus, supports the notion (e.g. Schindler *et al*., 2010; Bekkevold *et al*., 2011) that marine fish management needs to incorporate knowledge about individual population dynamics to allow sustainable exploitation of all substocks.

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TABLE 1. Parameter estimates for the reduced von Bertalanffy model. Values in parentheses denote 95% confidence intervals.

Parameter	Area	Estimate
K	All	0.380 (0.279, 0.481)
t_0	All	-1.94 (-2.57, -1.31)
$L_{\infty,autumn}$	North Sea	29.7 (28.3, 31.0)
$L_{\infty,autumn}$	Skagerrak	29.4 (28.1, 30.6)
$L_{\infty,autumn}$	Kattegat	26.5 (25.2, 27.7)
$L_{\infty,spring}$	North Sea	28.6 (27.4, 29.9)
$L_{\infty,spring}$	Skagerrak	28.3 (27.1, 29.5)
$L_{\infty,spring}$	Kattegat	25.4 (24.3, 26.5)

735 TABLE 2. Average condition of autumn and spring spawners by area. Values in parentheses denote

736 standard error of the estimate. Units are 10^{-3}g*$cm^{-3.26}$

Area	Autumn spawners	Spring spawners
North Sea	3.70 (0.03)	3.58 (0.03)
Skagerrak	3.73 (0.02)	3.52 (0.02)
Kattegat	3.45 (0.04)	3.19 (0.02)

737

738 Figure 1. The study area. Straight lines indicate ICES management subdivision areas, shading indicate
739 spawning grounds of the WBSS stock based on literature (Biester, 1979; Otterlind, 1987; Rosenberg
740 and Palmén, 2982) and information from local fishermen. The circle represents the main spawning
741 ground (Greifswalder Bodden; Biester, 1979)

742 Figure 2. The proportion of spring spawners by weight in abundance by year and statistical rectangle
743 (grayscale colours) as well as total abundance weight by statistical rectangle and year (bubbles, areas
744 are proportional to total catch weight but rescaled for each year, hence only within year comparisons
745 are possible).

746 Figure 3. Biomass of autumn (top) and spring (bottom) spawners per rectangle across years in the
747 North Sea (black symbols, black line), Skagerrak (grey symbols, grey line) and Kattegat (open
748 symbols, broken line). Lines are regression lines.

749 Figure 4. Left: annual centre of gravity for the autumn spawners (circles with grey thin lines) and
750 spring spawners (circles med black thick lines) size and numbers within circles indicate year as in
751 20xx. Right: average centre of gravity for age classes 1-5 wr, autumn spawners (circles with grey thin
752 lines) and spring spawners (circles med black thick lines) size and numbers within circles indicate age
753 (wr).

754 Figure 5. Ln(Catch in numbers) at age of autumn (left) and spring (right) spawners in the North Sea
755 (solid triangles, solid line), Skagerrak (open diamonds, dotted line) and Kattegat (open squares, dash
756 line). Lines are regression lines.

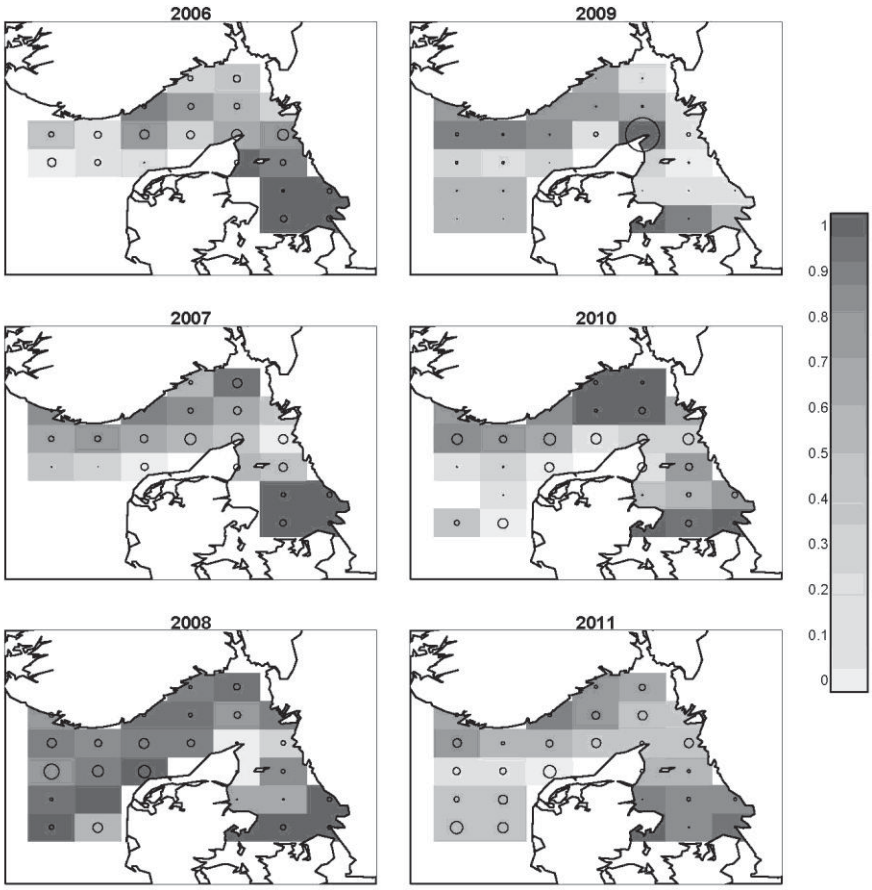
757 Figure 6. Predicted length at age for each area and type from the reduced von Bertalanffy model. Left:
758 Autumn spawners, Right: spring spawners. Black: North Sea and Skagerrak, grey: Kattegat. Solid line
759 denotes predicted length, hatched lines the 95% confidence interval around the prediction.

760 Figure 7. Residuals from the final von Bertalaffy model by year (growth anomalies). Autum spawners
761 (open symbols, hatched line) and spring spawners (closed symbols, solid line) in the North Sea (top
762 left), Skagerrak (top right) and Kattegat (bottom left).

763 Figure 8: Condition (C) of spring spawners vs condition of autumn spawners, by ICES rectangle, year
764 and age. Increasing size of bubbles indicates increasing age from 1 wr to 5 wr.

765

Figure 1.



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769 Figure 2.

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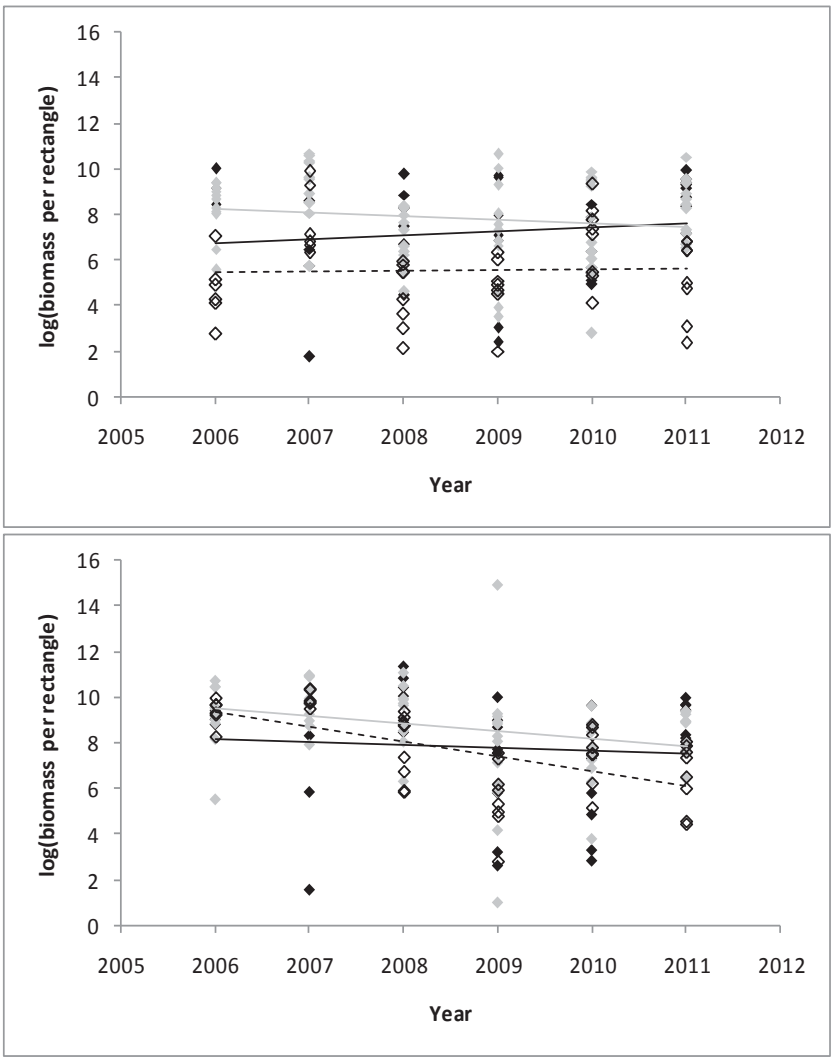

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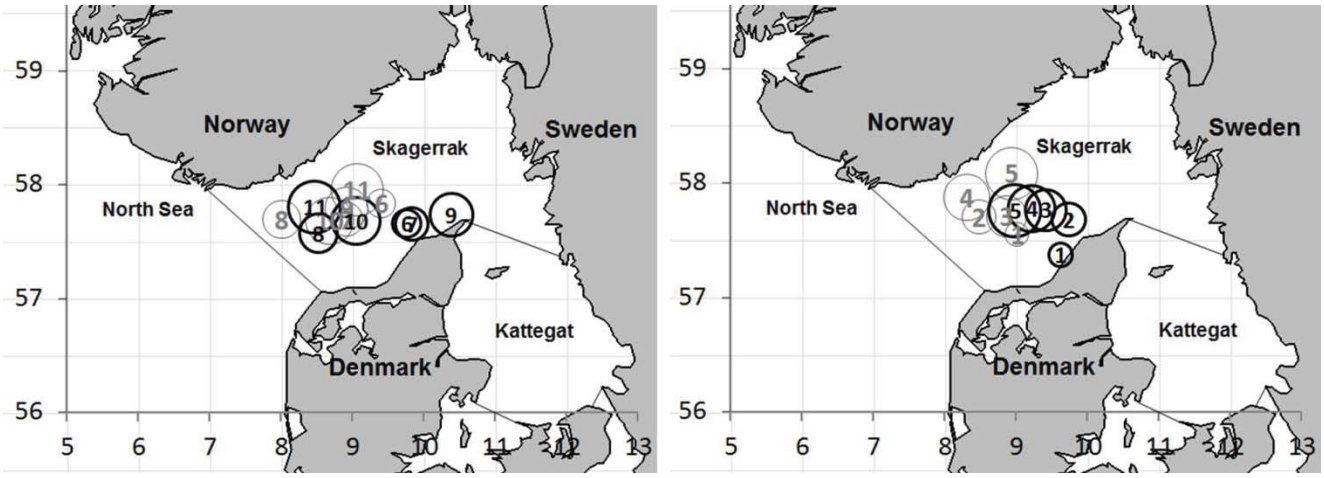

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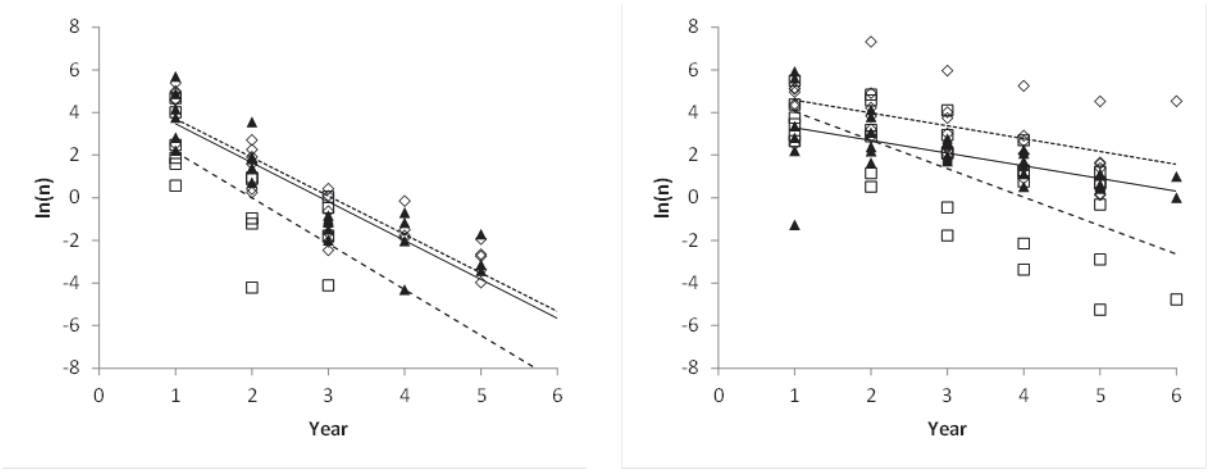

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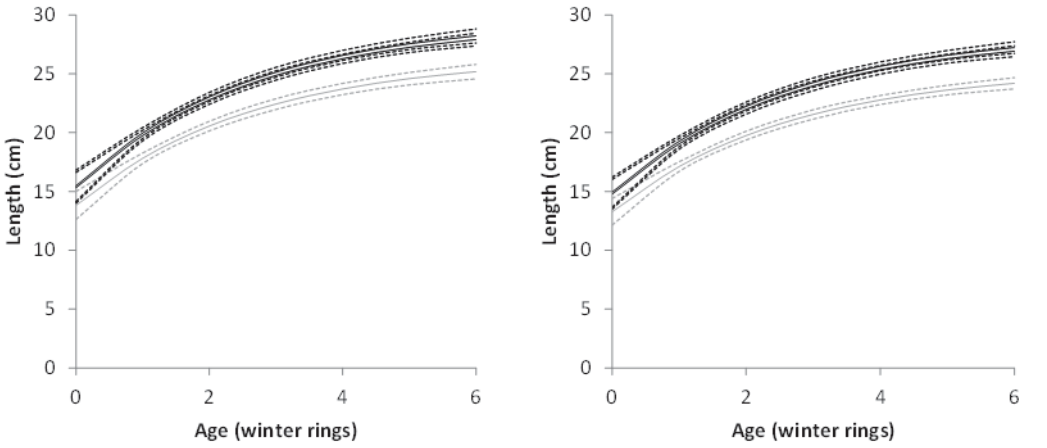

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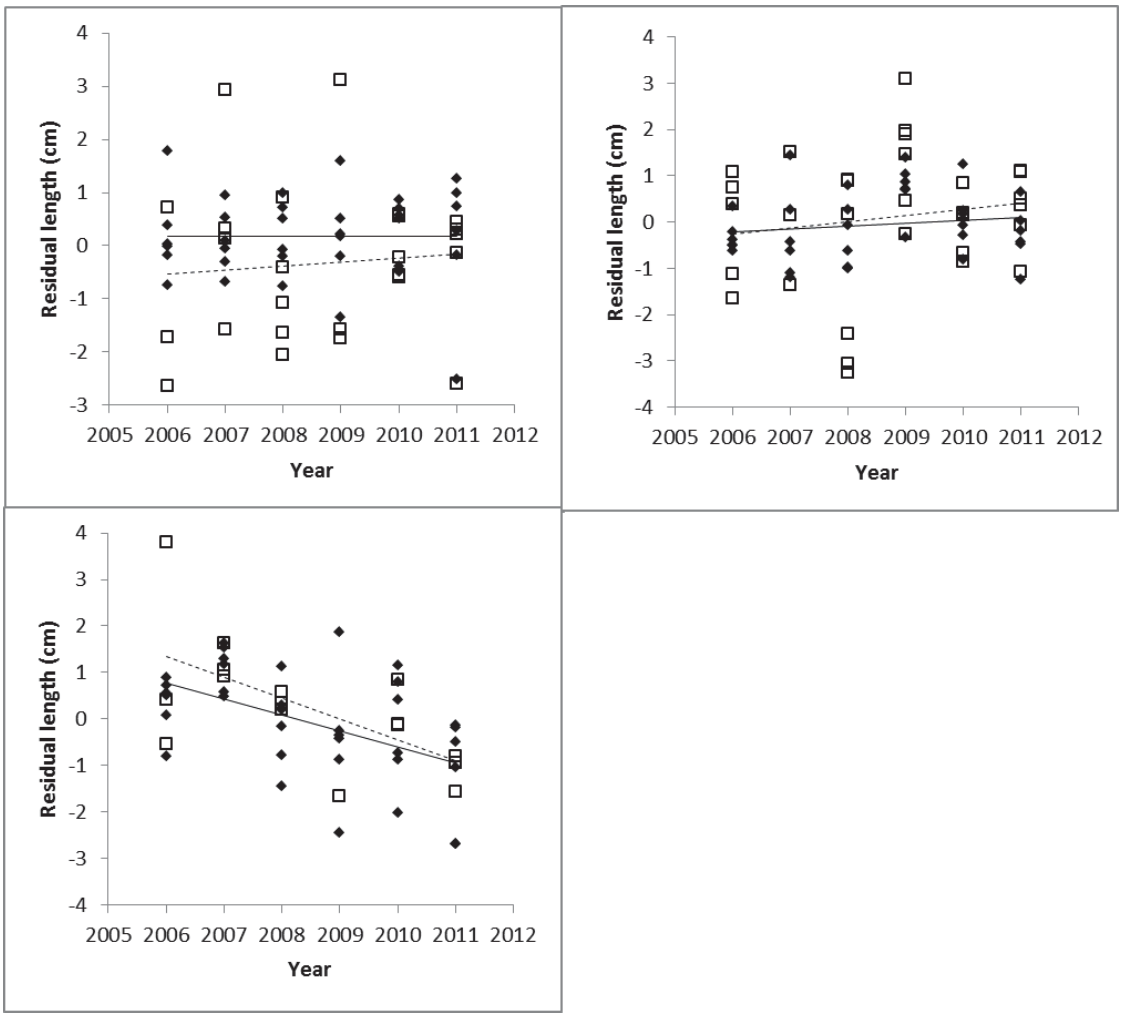

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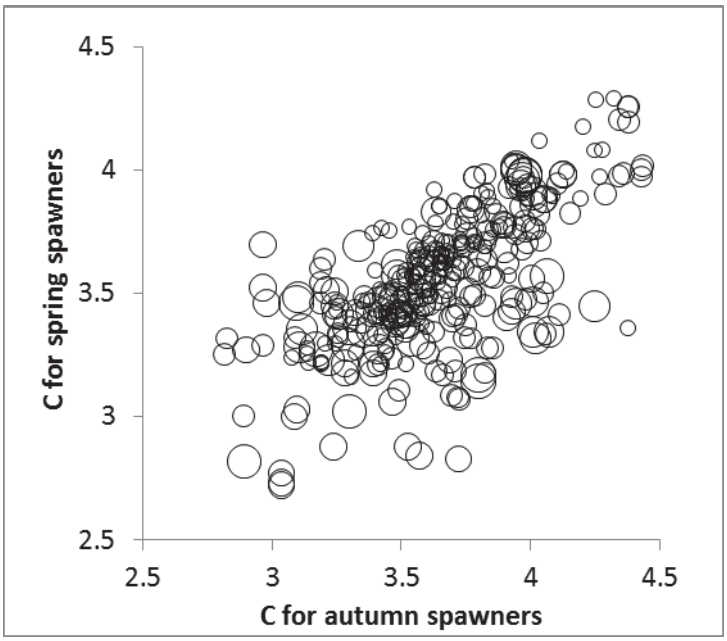
780 Figure 7.



781

782 Figure 8.